Chapter 7

Nesting Patterns, Reproductive Migrations, and Adult Foraging Areas of Loggerhead Turtles

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Monitoring trends in loggerhead turtle populations is critical to assessing population status and to developing and assessing conservation strategies. Presently, the most reliable estimates of sea turtle population size come from counts on nesting beaches. In addition to providing population estimates, nesting beach data also provide information on how reproductive effort is focused spatially and temporally. Several measured parameters are key to describing reproductive effort and to estimating the number of nesting females from nest count data. Among these parameters are clutch frequency, remigration interval, and nesting site fidelity (collectively referred to here as nesting patterns). These three key measures are intimately linked and have great bearing on the accuracy of the simple calculations used to derive nesting population estimates from numbers of nests. Although numerous authors have reported clutch frequency and remigration interval values for loggerheads at nesting beaches around the world, information on nesting site fidelity is less frequent in the literature, perhaps because of the difficulty of obtaining this measure.

Effective conservation programs for sea turtles require more than an understanding of nesting patterns and nesting population size. With regard to the adult life stage, information on migratory routes and foraging areas is also needed. The purpose of this chapter is to outline the loggerhead reproductive data necessary for guiding conservation programs. Here, the authors review available data on loggerhead nesting patterns, reproductive migrations, and adult foraging areas, and they evaluate deficiencies in understanding these aspects of loggerhead life history.

Nesting Patterns

For most of their lives, sea turtles are difficult, if not impossible, to census. However, one segment of each population predictably presents itself for counting, when adult females crawl from the water to nest. On some beaches, "saturation tagging" of all nesting females can lead to direct counts of individuals, but on other beaches that cover large expanses, these direct counts are not practical because of the difficulties in successfully intercepting all nesting turtles.

It is logistically feasible on most beaches to count the number of nests made each night during an early morning survey of the nesting beach (Schroeder and Murphy 1999). This count can then be used to determine both the number of adult females nesting annually and the number of breeding females in the population, provided two key parameters are known: (1) clutch frequency, defined as the number of nests deposited by a female during one reproductive season, and (2) remigration interval, defined as the number of years between reproductive seasons (Carr et al. 1978; Limpus 1985). Clutch frequency is sufficient to derive an estimate of annual numbers of breeding females, but remigration intervals are also needed to estimate the total number of breeding females in the population.

The tendency of a turtle to return to nest near the area where she nested previously, either within a season or in a previous season, is referred to as nesting site fidelity (also referred to as site fixity). Carr (1975) recommended the term "philopatry" for discussing the return to a broader geographic place (e.g., an island or a broad stretch of coastline) and the term "site fixity" (herein referred to as "nesting site fidelity") for discussing finer scale discrimination. Although nesting site fidelity is not a parameter that is directly used to calculate breeding female population size, knowledge of this parameter is necessary to evaluate the validity of values for clutch frequency and remigration intervals (Did a survey effort encompass enough beach to locate all of a turtle's nests?).

Clutch Frequency

Loggerheads deposit from one to seven clutches during a single nesting season (Table 7.1; Dodd 1988; Lenarz et al. 1981; Lund 1986; Talbert et al. 1980). This wide range may reflect both true variation and survey error. Error is expected to result when some nesting females are either not observed or not recognized every time they nest within a particular year on the survey beach.

Accurate determinations of clutch frequency require that every female on the survey beach be intercepted and documented each time she nests within a nesting season. This is seldom accomplished. Because a loggerhead can nest in approximately one hour, at any time during the night, and up to seven times over a span of three to four months (Dodd 1988) and hundreds of kilometers of beach (Encalada et al. 1998), it is reasonable to assume that some nesting attempts by each female might be missed. The accuracy of a clutch frequency determination will depend heavily upon survey completeness and on nest site fidelity among the turtles studied. Even if surveyed areas are large and nesting site fidelity is strong, females that have a nesting area centered near the edge of the surveyed area may still nest outside the surveyed area. This "edge effect" (Murphy and Hopkins 1984) will result in clutch frequencies that are biased low.

Determinations of clutch frequency rely upon the collection of information from uniquely marked individuals. Marking is most commonly accomplished through the use of various types of external flipper tags (Balazs 1999). With a typical internesting interval of about 14 days (Dodd 1988) and a maximum clutch frequency of six to seven nests (Lenarz et al. 1981; Lund 1986; Talbert et al. 1980), flipper tags must be retained for at least three to four months in order to assure that individual females are recognized each time they nest within a season. The loss of flipper tags over the course of a typical nesting season (several months) is low (0.5–1.3%; Limpus 1992) and is not likely to impede repeat identification of nesting females.

Several published methods to measure clutch frequency do not require that females be intercepted every time they nest. Some of these methods assume a predictable internesting interval and interpolate the number of "missed" nests per female based on observed nesting events during a nesting season (Frazer and Richardson 1985; Hughes 1974). Addison

Table 7.1.
The Mean Number of Clutches per Female (Clutch Frequency) per Reproductive Season at Various Loggerhead Rookeries around the World

Location	Number of Females	Observed Clutches per Season	Mean Clutch Frequency		Source
			Observed	Corrected	
Little Cumberland Island, GA, USA	427	—	—	4.1	10
Little Cumberland Island, GA, USA	36–62[a]	—	2.39–3.42[a]	2.81–4.18[a]	3
South Brevard County, FL, USA	236	1–3	2.05	3.24	2
Key Island, FL, USA	521	1–7	1.84	3.9	1
Cape San Blas, FL, USA	111	1–4	1.35	—	7
Colombia (Caribbean coast)	80	1–4	1.12	—	6
Zakynthos, Greece	148	1–3	1.18	—	9
Tongaland, Natal, Africa	241–321[b]	1–5	1.81–2.29[b]	3.65–4.21[b]	4
Miyazaki, Japan	199	1–2	1.10	—	5
Yakushima Island, Japan	358	1–6	2.06	—	11
Mon Repos, Australia	1,207	1–6	2.91	3.41	8

Source Key: 1. Addison 1996a, 1996b. 2. L. M. Ehrhart, unpublished data. 3. Frazer and Richardson 1985. 4. Hughes 1974. 5. Iwamoto et al. 1985. 6. Kaufmann 1975. 7. M. M. Lamont, unpublished data. 8. Limpus 1985. 9. Margaritoulis 1982, 1983. 10. Murphy and Hopkins 1984. 11. Nishimura 1994.

Note 1: The corrected frequencies adjust for turtles that were either known or suspected to have nested both inside and outside of the study site.

Note 2: FL = Florida; GA = Georgia.

[a]Range of annual values over a 10-year period.

[b]Range of annual values over a four-year period.

(1996b) used only nesting turtles that were intercepted more than once to estimate a "corrected" clutch frequency. Addison's corrected clutch frequency of 3.9 nests/season/female was substantially higher than the empirically measured frequency of 1.8 nests/season/female (Table 7.1). Murphy and Hopkins (1984) created a stochastic frequency distribution of nesting based on the date of initial nesting in a season and the average internesting interval for all females encountered over a period of many years on one nesting beach. The trend of a steadily rising number of nests that was created as this simulated nesting season progressed was then reversed at the typical midpoint of the season. A clutch frequency of 4.1 nests/season/female was determined by dividing the total number of nests generated from the stochastic frequency distribution by the number of females used to create it. Although these methods are helpful in overcoming the logistic difficulties of intercepting females every time they nest, the assumptions on which they are based and the resulting data need to be periodically assessed and verified.

Several other methods of determining clutch frequency warrant further investigation or experimentation. Rostal et al. (1991, 1997) approached the question in a two-fold manner—by examining the reproductive tracts of gravid Kemp's ridleys via ultrasonography and by monitoring reproductive hormones over the course of the nesting season. Both methods resulted in a higher estimated clutch frequency for Kemp's ridleys than that previously reported from mark-recapture studies and may well represent a more accurate determination. Recent advances in satellite telemetry potentially hold promise as tools for assessing clutch frequency. Satellite transmitters with appropriate sensors, similar to time-depth recorders used to gather data on haul-out behavior of walruses and pinnipeds, could be developed (Bengston and Stewart 1992; Jay et al. 2001). Deployed at the

Table 7.2.
Years between Successive Nesting Seasons (Remigration Intervals) for Various Loggerhead Rookeries around the World

Location	Number of Remigrations	Remigration Interval: Range	Observed Mean	Corrected Mean	Source
Little Cumberland Island, GA, USA	242	1–6	2.54		5
South Brevard County, FL, USA	161	1–7	2.71		1
South Brevard County, FL, USA	187	1–15	3.69		2
Tongaland, Natal, South Africa	740	1–9	2.58		3
Queensland, Australia	1,112	1–9	2.98	3.48	4

Source Key: 1. Bjorndal et al. 1983. 2. L. M. Ehrhart, unpublished data. 3. Hughes 1982. 4. Limpus 1985. 5. Richardson et al. 1978.

Note 1: The corrected mean was adjusted to account for tag loss.

Note 2: FL = Florida; GA = Georgia.

start of the nesting season, these tags would generate remotely sensed data that could yield information on the number of emergences over the course of the nesting season.

In addition to varying between beaches (see Table 7.1), clutch frequency is also likely to vary between years (Frazer and Richardson 1985). Clutch frequencies also vary among individuals, with remigrants having higher clutch frequencies than recruits (Limpus 1985; Lund 1986). Thus, interannual variation in the proportion of remigrants and recruits is likely to result in annual variation in clutch frequency. Events not related to a physiological reproductive capability can cause nesting turtles to fall short of their potential complement of clutch deposits, thus decreasing clutch frequency. These events could include mortality of females during the internesting period and disturbances on nesting beaches (e.g., human activity, beachfront lighting, coastal armoring; Lutcavage et al. 1997).

The importance of obtaining accurate estimates of clutch frequency, with appropriate error statistics, cannot be overstated. This value is the divisor used to convert the number of nests to the number of nesting females and can have profound effects on the estimate of nesting females. For these reasons, and for the reasons noted above with regard to shifts in clutch frequency, the authors believe that comprehensive monitoring programs should incorporate periodic assessments of clutch frequency in order to ensure accuracy.

Remigration Interval

Long-term mark-recapture studies on most of the world's principal loggerhead nesting beaches have shown that loggerhead remigration intervals range from one to nine years (Dodd 1988). The mean observed remigration interval ranges from 2.5 to about 3.0 years (Table 7.2). Limpus (1985) applied a correction factor to his data to account for tag loss and reported a 3.48-year remigration interval for Australian loggerheads. Richardson et al. (1978) and Hughes (1982) reported a high proportion of turtles that were never documented to nest in a subsequent season. However, Hughes (1982) cautions that a major cause of the uncertainty in assessing remigration intervals is likely to be tag loss (see below for further discussion).

Mortality also plays an important role in determining whether females will return to nest in a subsequent season. High mortality in the adult female portion of the population (e.g., extensive fishing pressure near nesting beaches, along migratory routes, or at resident foraging areas) can dramatically affect the proportion of the population that is available (alive) to remigrate and nest in subsequent nesting seasons. Population modeling efforts for the intensively studied eastern Australian loggerhead population indicate that population stability requires high adult survivorship over an extended period of time and breeding over multiple nesting seasons (C. Limpus, pers. comm.). Thus, the low remigration rates observed at a number of important loggerhead rookeries may be an artifact of unnaturally high levels of mortality combined with the practical difficulties of long-term marking of individuals.

Remigration intervals are most commonly determined by flipper-tagging nesting females and by conducting multiyear nesting beach surveys in order to intercept and identify tagged females at least once each season they nest. The onus of intercepting individual females every time they nest over the course of the nesting season (as required for determining clutch frequency) is not necessary when determining remigration intervals. Flipper tag loss over the average remigration period (two to three years) ranges from 10 to 50% (Limpus 1985) and becomes a greater source of error in determining remigration intervals than it is in determining clutch frequency. Tag loss is likely to result in underestimated remigration intervals (by excluding long-interval turtles more likely to lose tags) and overestimated numbers of breeding females. The increasing use and success of subdermal passive integrated transponder (PIT) tags as a permanent marker in sea turtles should allow researchers to overcome the tag loss factor; however, problems with the compatibility of available PIT tag readers and PIT tags could affect research results.

Remigration intervals are not fixed for individuals. Nesting females may shift from one cycle (e.g., two years) to another (e.g., three or four years) and may shift multiple times during the course of their breeding lifetime (Hughes 1974; Limpus 1985). The proportion of recruits and remigrants that nest during a given year and the remigration intervals characteristic of the population may change over time. Variation in mortality rates at nesting beaches, on foraging grounds, or along migratory routes plays a role in determining what proportion of adult females nest during one season and what proportion eventually remigrates (Frazer 1984). Annual variation in the quality of forage may lengthen or shorten remigration intervals (Limpus and Nicholls 1988). Just as periodic evaluation of clutch frequency is needed, periodic evaluation of remigration interval is also needed to ensure accurate estimates of the total number of breeding females in a population.

Nesting Site Fidelity

Nesting site fidelity is most commonly measured in terms of the mean distance between nest sites of individual turtles, either within or between seasons. Whereas there are a number of long-distance within- and between-season movements documented in the literature (see e.g., Iwamoto et al. 1985; LeBuff 1974; Sea Turtle Protection Society of Greece 1995; Stoneburner and Ehrhart 1981), the typical distance between nest sites is 5 km or less. Loggerheads can exhibit strong site fidelity (Table 7.3). Ehrhart (1980) reported that 21% of turtles observed returning at multiyear intervals were less than 1.0 km away from their first observed nesting site. Mean distance between nest sites of individual loggerheads, within and between seasons, is similar between loggerhead populations (Table 7.3).

Nesting site fidelity can vary among females, with some individuals always nesting on a relatively small section of a particular nesting beach (stronger nesting site fidelity) and others spreading their nests over a larger section of beach (weaker nesting site fidelity). Turtles with weaker nesting site fidelity can contribute to inaccuracy in determining either clutch frequencies or remigration intervals. For example, at Potamakia Beach, Greece, loggerheads that were documented nesting more than once during one year (stronger nesting site fidelity) were significantly more likely to be documented as remigrants in subsequent years than were individuals either observed nesting only once (weaker nesting site fidelity) or observed during abandoned nesting emergences (Hays and

Table 7.3.
Distances between the Nest Sites of Individual Loggerheads from Various Rookeries around the World

Location	Number of Observations	Mean (km)	Range (km)	Source
Tongaland, Natal, South Africa[a]	505	< 4.0	0–12	2
Hutchinson Island, FL, USA[a]	21	17.48	0.2–95.2	5
Cape Canaveral, FL, USA[a]	394	6.89	0–32.3	1
Mon Repos, Australia[a]	150	0.382	0.025–1.25	4
Jupiter Island, FL, USA[a]	803	3.0	0–14.0	3
Tongaland, Natal, South Africa[b]	85	3.47	0–11.6	2
Cape Canaveral, FL, USA[b]	39	5.47	0–27.94	1

Source Key: 1. Ehrhart 1980. 2. Hughes 1974. 3. Lund 1986. 4. Limpus 1985. 5. Worth and Smith 1976.

Note: FL = Florida.

[a]Nest sites within a nesting season.

[b]Nest sites between seasons.

Sutherland 1991). Similarly, Richardson et al. (1978) calculated a 49% remigration rate for recruits (turtles not previously tagged when first observed at Little Cumberland Island, Georgia) and a 70% remigration rate for loggerheads with an established remigration pattern. The lower remigration rate for previously untagged turtles may indicate that some portion of these turtles had nested elsewhere previously and/or nested elsewhere following the observed nesting at this particular beach.

Logistic difficulties in intercepting nesting females (even during comprehensive surveys) and the added problem of tag loss both introduce bias in the evaluation of nesting site fidelity. Cooperation and data sharing among projects on adjoining beaches can help reduce some of these biases.

Anthropogenic factors also complicate the evaluation of nesting site fidelity. Nesting turtles that are continuously thwarted by disturbances may (1) move to another nesting site, (2) emerge more frequently, or (3) attempt to nest in unsuitable areas (Murphy and Hopkins-Murphy, unpubl. data). Thus, the mean nesting site fidelity of a population could change with increasing disturbances such as development and human activity. The potential for variation in nesting site fidelity over time reemphasizes the need to periodically assess clutch frequency and remigration intervals to ensure accuracy.

Reproductive Migrations and Adult Foraging Areas

Much of what researchers have learned about the life history and behavior of adult loggerheads has been gleaned from the brief period when adult females are present on nesting beaches. However, conserving loggerheads requires additional information extending beyond the nesting beach to include aspects of their life at sea. Of particular importance is an understanding of where adult loggerheads reside during the nonbreeding season and how they move between foraging areas, courtship areas, and nesting beaches. Most research in this regard has been to identify areas that females inhabit during the nonnesting season and the routes they take to reach these areas (e.g., Bell and Richardson 1978; Hughes 1974; LeBuff 1990; Margaritoulis 1988; Meylan et al. 1983). More recently, research has broadened to include studies of females and males migrating to mating and nesting grounds, and studies of resident adults, both males and females, at their foraging sites (e.g., Limpus et al. 1992; Sakamoto et al. 1997).

The classical means of elucidating sea turtle migrations is to tag nesting females and record the distant recovery of those tags when turtles strand or are captured. These tag return data are available from virtually all the major loggerhead nesting populations. Results of these studies indicate that adult females make both short- and long-distance postnesting migrations. No breeding loggerheads appear to be "nonmigratory" (Limpus 1992).

Recapture data provide point-to-point movement information but offer little insight into travel routes or into whether the point of recovery is an actual destination. As a result, recaptures of tagged turtles may not provide a complete picture of the range of foraging areas (Limpus 1985). Additionally, tag recaptures away from the nesting beach should be interpreted with an understanding that recapture rates and locations are frequently biased by variable recapture methods (e.g., reporting of flipper-tagged turtles captured in U.S. shrimp trawls dropped significantly during the years of controversy over the implementation of turtle excluder devices). Despite the limitations, flipper tag data are important in formulating hypotheses that can be further evaluated using additional techniques.

The advent of satellite telemetry has dramatically increased knowledge of loggerhead migratory behavior. Research efforts using satellite telemetry to determine loggerhead reproductive migrations are under way in the Mediterranean, South Africa, Japan, Australia, Brazil, Bahamas, and the United States (A. Bolten, pers. comm.; Hays et al. 1992; C. S. Hopkins-Murphy, pers. comm.; Limpus, pers. comm.; B. Schroeder, unpubl. data; Sakamoto et al. 1997). The principal focus of these studies has been to identify postnesting migration routes and adult foraging areas.

Approximately 100 postnesting female loggerheads have been satellite tracked worldwide. Data acquired through the use of satellite tags may include various diving measures, dive profiles, and water temperature, as well as standard data such as latitude/longitude, time, and a measure of the accuracy of the transmitted location. Ideally, satellite telemetry and flipper-tagging programs should work to complement each other.

Based on published and unpublished satellite telemetry data and flipper tag return data, a number of conclusions can be drawn with regard to loggerhead postnesting migratory behavior and loggerhead adult foraging areas.

- Postnesting females depart from the nesting beach immediately following deposition of the last clutch, in most cases within 24 hours.
- Postnesting females typically make directed migrations. Random wandering does not appear to be a characteristic behavior. This evidence contradicts the conclusion of Hendrickson (1980) that loggerheads did not appear to exhibit directed movements during reproductive migrations.
- The migratory route taken may be coastal or may involve crossing deep oceanic waters; an oceanic route may be taken even when a coastal route is an option.
- All females dispersing from a rookery do not necessarily follow the same migratory path, even if the foraging destinations are similar.
- Ocean currents may affect migration routes, resulting in temporary course adjustments. Postnesting females sometimes swim against prevailing currents.
- Postnesting loggerheads take up residence in discrete foraging areas. These areas are relatively small in size, on the order of tens of square kilometers, and are located on continental shelves.
- Postnesting females may move among a few preferred foraging sites within the larger foraging area.
- Adult females exhibit strong site fidelity to foraging areas and have been observed to return to these sites over the course of many breeding seasons.
- Some U.S. loggerheads migrate to two successive, seasonally dependent foraging areas. For these turtles, initial postnesting migration is north, and a second migration is directed south as northern waters cool.
- Foraging areas may be located relatively near the nesting beach or thousands of kilometers distant and may be located within a different nation than the nesting beach.
- The migratory route may be wholly contained within the waters of one nation or

Table 7.4.
Locations of Principal Foraging Areas of Postnesting Loggerheads

Nesting Beach	Principal Resident Foraging Areas	Source
Japan	East China Sea, South China Sea	6, 7, 16
Eastern Australia	Eastern Australia, Coral Sea, southern and eastern Papua New Guinea, Gulf of Carpentaria	9
Southeast Africa	Mozambique, Tanzania (mainland), Zanzibar, Madagascar	4, 5
Florida east coast, USA	Bahamas, Cuba, Mexico, Florida coastal waters, Gulf of Mexico	3, 12, 17
Florida west coast, USA	Florida West Coast, Cuba, Mexico, Gulf of Mexico	17
Georgia and South Carolina, USA	USA, southeast and mid-Atlantic coast	1, 13, 14
Masirah Island, Oman	Arabian Gulf, southern Arabian peninsula westward to Yemen, Gulf of Oman east to Pakistan	15
Cay Sal, Bahamas	Southern Bahamas	2
Brazil	Coast of Brazil	10
Greece	Tunisia, Adriatic Sea, eastern and western Mediterranean	8, 11

Source Key: 1. Bell and Richardson 1978. 2. A. Bolten and K. Bjorndal, unpubl. data. 3. L. Ehrhart, unpubl. data. 4. Hughes 1995. 5. Hughes et al. 1967. 6. Iwamoto et al. 1985. 7. Kamezaki et al. 1997. 8. Lazar et al. 2000. 9. Limpus 1985, 1992. 10. Marcovaldi et al. 2000. 11. Margaritoulis 1988. 12. Meylan et al. 1983. 13. S. Murphy, unpubl. data. 14. Plotkin and Spotila 2000. 15. P. Ross, pers. comm. 16. Sakamoto et al. 1997. 17. B. Schroeder, unpubl. data.

Note: From various rookeries around the world, as identified from tag returns and satellite telemetry data.

may involve travel through the waters of other nations.

- Loggerheads do not necessarily nest at the nesting beach located closest to their home foraging area.
- Foraging areas of female loggerheads from different nesting beaches (including genetically distinct subpopulations) within a region may overlap.

Information on the location of foraging areas is available for many of the major loggerhead rookeries (Table 7.4). Although researchers are beginning to understand migratory routes and destinations of postnesting loggerheads, detailed habitat characterization of adult foraging areas is lacking. It does not appear that adult loggerheads from regional rookeries converge at a few discrete sites; rather, their resident foraging areas are widespread (Table 7.4). This dispersal of foraging areas challenges efforts to ensure their protection. Limpus (1992), in describing the situation for eastern Australia adult loggerheads, said, "Even the Great Barrier Reef Marine Park, the largest marine conservation area in the world, is not large enough to contain an entire population of *C. caretta*." Geographically extensive feeding areas for the adult segment of the population are undoubtedly characteristic of all major loggerhead rookeries.

Long-term tagging studies of large immature loggerheads on foraging grounds in eastern Australia are providing evidence that long-term fidelity to a resident foraging area has its origins in an imprinting to the feeding ground where a turtle reaches sexual maturity (Limpus 1994). This underscores the need to ensure that these habitats are protected and that threats at these sites are addressed.

While data regarding migratory behavior of adult females are accumulating, studies of reproductive migratory behavior of adult males are rare, and the published literature is lacking in this regard. Limpus's recent studies in Australia of loggerheads on their foraging grounds indicate that males migrate to courtship and mating areas and then return with high site fidelity to their foraging areas, while females continue on to nesting beaches (C. Limpus, pers. comm.). In the western Atlantic, Henwood (1987) documented seasonal differences in the abundance of adult males in the near-shore waters off central Florida, with males present in significantly higher numbers in the months immediately preceding the onset of the nesting season. This is similar to what Limpus reported for male loggerheads on the other side of the globe. Henwood (1987) suggested that the presence of the same individual males in the vicinity of nesting beaches during consecutive reproductive seasons may indicate annual breeding, although the reproductive condition of the males was not verified through laparoscopy or other means.

A significant assemblage of adult male loggerheads resides year-round in Florida Bay at the southern terminus of the Florida peninsula, and studies of the migratory behavior of these turtles are under way (Schroeder, unpubl. data). The Florida Bay data suffer from the same lack of confirmation of individual reproductive condition. Clearly, more work is needed to understand the behavior of the male component of the population, especially relative to reproductive periodicity.

Conclusions

Information relative to nesting patterns, reproductive migrations, and adult foraging areas is critical to understanding and conserving global loggerhead populations. Clutch frequency, remigration interval, and nesting site fidelity are key variables that need to be regularly evaluated to ensure that population estimates derived from nesting beach data are accurate. Limitations in measuring clutch frequencies and remigration intervals can result in profound overestimates of abundance of breeding females. There are few recent assessments of these key measures at the principal loggerhead rookeries around the world. Increased focus on the reproductive periodicity and migratory movements of adult male loggerheads is needed for all the major nesting assemblages. Comprehensive studies similar to the long-term in-water studies on loggerheads in eastern Australia are needed at all of the other major regional foraging sites for this species. The integration of data on migratory routes and foraging areas, as part of an ecosystem-based assessment, is also needed to ensure long-term habitat protection.

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